**Abstract**

1. Studies on ecological communities often address patterns of species distribution and abundance, but few consider uncertainty in counts of both species and individuals when computing diversity measures.
2. We evaluated the extent to which imperfect detection may influence patterns of taxonomic, functional and phylogenetic diversity in ecological communities.
3. We employed a hierarchical Bayesian N-mixture model to estimate the true abundance of fruit-feeding butterflies sampled in canopy and understory strata in a subtropical forest. We then developed a tool to calculate how much information is hidden when uncertainty in counts of species and individuals is not considered when estimating diversity.
4. We found that detection probability was asymmetric between strata and there was a loss of information for all diversity measures when species detectability was ignored. Incidence-based diversity measures were less affected by imperfect detection than abundance-based diversity measures, and the canopy showed greater bias in hidden diversity among sites than did the understory. Furthermore, detection probability did not show phylogenetic signal, but was associated with dispersal traits in the canopy and reproductive traits in the understory.
5. Ignoring imperfect detection may lead to false negative or positive environmental effects, because the effect of imperfect detection on diversity may not be evenly distributed across environmental gradients. Whenever detection probability varies along an environmental gradient, we recommend that corrected detection be used to compute diversity measures instead of raw data, especially for abundance-based data. Such a correction should be carried out independently of whether detection probability shows phylogenetic signal or not, or is correlated with traits related to detection. The tool developed in this study can help to evaluate when the non-inclusion of uncertainty can promote an erroneous interpretation of diversity-environment relationships.

**Key-words:** assemblage structure, community hierarchical models, detection probability, environmental gradients, fruit-feeding butterflies, functional traits, phylogenetic diversity.

**Introduction**

The number of species present in a given area is the most basic diversity measure in community ecology. But since species richness does not consider heterogeneity in species counts among sites, it may not fully capture mechanisms determining community assembly patterns. Abundance measurements are related to extinction and survival probabilities, species interactions and ecosystem functioning (Dorazio, Connor, & Askins, 2015; Joseph, Elkin, Martin, & Possingham, 2009; Kéry, Royle, & Schmid, 2005; Yamaura et al., 2011). However, both species and individual counts are often incomplete since all species or individuals are not perfectly observed in the field (i.e. they are imperfectly detected during sampling), and different species have distinct probabilities of being detected (Boulinier, Nichols, Sauer, Hines, & Pollock, 1998; Danilo Bandini Ribeiro, Williams, Specht, & Freitas, 2016). Classical community analyses commonly ignore imperfect detection, for both incidence and abundance-based approaches, as well as its effects on diversity measures (Iknayan, Tingley, Furnas, & Beissinger, 2014; Broms, Hooten, & Fitzpatrick, 2015; Jarzyna & Jetz, 2016; Si et al., 2018).

At the community level, species share evolutionary history and show phenotypic variation. These two features of species are widely used to infer historical and/or ecological mechanisms determining community assembly patterns (Duarte, Debastiani, Carlucci, & Diniz-Filho, 2018; Graham & Fine, 2008; Webb, Ackerly, McPeek, & Donoghue, 2002). The number of studies analyzing phylogenetic or functional diversity patterns has increased over recent decades, jointly with the number of alternative diversity metrics available to assess such patterns (de Bello et al., 2015; Tucker et al., 2017). Nevertheless, few studies have quantified the role and magnitude of the effects of imperfect detection on distinct facets of diversity (Jarzyna & Jetz, 2016; Roth, Allan, Pearman, & Amrhein, 2018; Si et al., 2018). Si et al. (2018) found that both phylogenetic and functional diversity measures of avian assemblages tended to be higher than expected when imperfect detection was taken into account. Under this scenario, increased diversity values were likely to result from the inclusion of formerly undetected phylogenetically or functionally unique species in assemblages, implying that an ecologically important part of the assemblages was being neglected when imperfect detection was not incorporated into diversity estimation (Jarzyna & Jetz, 2016). Hence, if imperfect detection is disregarded in the calculation of diversity, the mechanisms that assemble communities may be erroneously inferred (Si et al., 2018). Furthermore, Frishkoff et al. (2017) found that ignoring imperfect detection could lead to biased estimates of phylogenetic signal in relation to habitat use, and even more so when species-specific detection probabilities vary in response to environmental gradients. The inclusion of imperfect detections showed a low effect on measures of functional diversity and composition for a plant assemblage along an elevational gradient (Roth et al., 2017). However, the authors found that some traits could be less detected and that species at low elevations are more likely to be missed during sampling (Roth et al., 2017).

Insects are the most species-rich taxa of world, which poses a major challenge for ecologists interested in evaluating insect diversity patterns (Thomas, 2005). Among insect groups, butterflies are considered important biological indicators due their short life-cycle and high sensibility to changes in environmental features (New, 1997, Brown & Freitas, 2000). Nonetheless, in cases where variation in species detection probabilities is found in natural assemblages, failure of accounting for imperfect detection might lead to poor conservation and management decisions (Banks-Leite et al., 2014; Benoit, Jackson, & Ridgway, 2018). Fruit-feeding butterflies are a conspicuous guild of tropical butterflies that feed on rotting fruit, carrion or plant exudates (DeVries, 1988) and represent about 50 – 75% of nymphalid diversity in the Neotropical region (Brown, 2005). Due their feeding habit, these butterflies can be sampled with passive and standardized methodologies such as bait traps (Freitas et al., 2020). Unlike other methods to sample butterflies (entomological nets or transect counts), bait traps avoid bias related to variation in observer or personal expertise about species detection (Boulinier et al., 1998, Kéry & Plattner, 2007, Ribeiro et al., 2016).

Population dynamics of butterflies is particularly susceptible to spatial and temporal fluctuations (Checa, Rodriguez, Willmott, & Liger, 2014). Assemblages of fruit-feeding butterflies show high vertical stratification (Devries, 1988; DeVries, Alexander, Chacon, & Fordyce, 2012; Ribeiro & Freitas, 2012; Santos, Iserhard, Carreira, & Freitas, 2017), with the canopy generally being more diverse than understory. Canopies tends to exhibit faster species accumulation curves than understories (DeVries et al., 2012; Devries & Walla, 2001) and generally have higher values for sampling coverage (Santos et al., 2017). The faster species accumulation for canopies could be related to the behavior of individuals that occupy this stratum (DeVries et al., 2012). Canopy-dwelling butterflies, like those of Charaxinae and Nymphalinae, possess traits that confer high flight mobility (Chai & Srygley, 1990; Devries & Walla, 2001; Hill, Hamer, Tangah, & Dawood, 2001), which may lead to inaccurate individual count estimates and therefore some bias in the observed assemblage patterns in canopy habitats. On the other hand, individuals sampled in the understory tend to be more habitat-specialists, making them more easy to detect. Moreover, since microclimatic and seasonal variation in environmental conditions may ultimately determine the spatial distribution of species (Checa et al., 2014; Nowicki, Settele, Henry, & Woyciechowski, 2008; Pellet, 2008), such climatic fluctuations might lead to imperfect detection of fruit-feeding butterfly assemblages because they can affect flight activity and the life-cycle of individuals (Ribeiro & Freitas, 2011).

In this study, we aimed to analyze the extent to which imperfect detection, assessed by the estimates of the true abundance of species, can lead to changes in observed patterns of taxonomic, functional and phylogenetic diversities of butterflies living in different forest strata (canopy *vs.* understory). We expected that: (i) if variation in detection probability is constant between strata, the observed pattern will not change (Fig 1a, b), but if variation in detection probability differs between strata, the pattern can be erroneously inferred (Fig 1c, d); (ii) assemblages will exhibit greater phylogenetic or functional clustering if low values of detection probability are shared by phylogenetically or functionally closely related species, respectively, due to the inclusion of redundant individuals in the assemblages; (iii) if detection probability varies between canopy and understory, the canopy will have greater bias in diversity estimates than the understory for all diversity patterns, due the characteristics of the individuals. Under this scenario, inferences made about fruit-feeding butterfly diversity of forest strata may be erroneous if imperfect detection in count data is not taken into account in the analysis.

**Material and Methods**

*Study sites and sampling procedures*

The study site was located in Floresta Nacional de São Francisco de Paula (FLONA-SFP; centered at 29°25’22’’S, 50°23’11’’W) in Southern Brazil. FLONA-SFP comprises an area of 1,615 ha in the Atlantic Forest biome and is composed of Mixed Ombrophilous Forest with the presence of *Araucaria* *angustifolia* (Bertol.) Kuntze, as well as patches with *Pinus* sp. and *Eucalyptus* sp. plantations (ICMBio, 2020). The climate of the region is temperate without a dry season, and with annual mean rainfall near 2,000 mm and an annual average temperature of 14.5°C (Sonego, Backes, & Souza, 2007).

Fruit-feeding butterfly assemblages were sampled between November 2016 and March 2017, that correspond to summer season at Southern Hemisphere and which is the best period of the year for sampling butterflies in the Atlantic Forest (Iserhard, Romanowski, Richter, & Mendonça, 2017). We adopted standardized methods for sampling fruit-feeding butterflies in the Neotropical region (Freitas et al., 2020), that consist in install five traps per sampling unit, which were baited with a mixture of mashed banana and sugarcane juice (Freitas et al., 2020). We performed monthly surveys at six sites of native forest within FLONA-SFP for five months. In each month, the traps remained open for eight to ten consecutive days and every 48h the traps were checked and the bait replaced totalizing a sampling effort of the 1260 trap-days (10 traps × 6 sampling units × 21 days). In each site we sampled the assemblages of fruit-feeding butterflies in the canopy (~15 m above the ground, inside canopy tree crowns) and in the understory (1.5 m above the ground) and each stratum was considered as one independent sampling unit. In every trap checking, we measured the temperature of the base of each trap using an infrared thermometer (GM-300, Benetech®).

*Community model for abundance data*

We employed a modification of the DRY (Dorazio-Royle-Yamaura) model (Kéry & Royle, 2016; Yamaura et al., 2011; Yamaura, Kéry, & Andrew Royle, 2016) to estimate uncertainties in the individual counts for fruit-feeding butterflies. The modifications allows that the model estimates the mean abundance (λik) and detection probability (pijk) for each stratum (Zipkin, Andrew Royle, Dawson, & Bates, 2010). We assumed that local abundance remained unchanged during the survey (i.e. closure assumption, Kéry et al., 2005) since we sampled in a narrow-time window, and that mean abundance and detection probability were independent among species. Abundance for each species *k* at each site *i* is a latent variable (i.e. imperfectly observed) called *Nik*, which follows a Poisson distribution:

where *λik* is the expected abundance. We assumed that *λik* varied among sites depending on species random effects and if point *i* was in the canopy (Strata = 0) or the understory (Strata = 1), thus allowing species-level effects to differ between the two strata (Zipkin et al., 2010). We also included a slope for the mean temperature obtained from base of the traps of each site *i* (Temp) and add two random site effects, because samplings were repeated in time (sampling months, sm) in the same sampling units (su), and hence their measures are not independent within them. We fit the model for biological process using a log-link function, as follows:

where β.can and β.und are the species-specific intercepts for canopy an understory, respectively, β1 is the slope for the temperature effect, *s* and *m* are the random effects for six sampling units and five sampling months.

We describe the detection process as:

where the number of detected individuals *yijk* during visit *j* was obtained with *Nik* trials and a probability of successful detection *pijk*. The detection history *yijk* > 0 indicates that the species *k* (1, 2, ..., 35) was observed in site *i* (1, 2, ..., 12) during the sampling occasion *j* (1, 2, …, 5), while *yijk* = 0 implies the species was undetected. We modeled detectability as a logit-linear combination of species-specific detection probabilities dependent on stratum, and two covariates:

where α.can and α.und are the species-specific intercepts for canopy and understory, respectively, and α1 is the linear effects of the day of sampling (transformed to Julian date) and α2 is the linear effects of the temperature by day.

All covariates for biological and observation process were standardized before perform the Bayesian model. We defined species-specific parameters for each strata and covariates as coming from normal hyper-distributions, e.g., β.cank ~ Normal (µβ.can, τβ.can), being that these priors describe the heterogeneity among species. We determined vague priors for the hyper-parameters that define the mean µβ.can and precision τβ.can at the community-level, such that µβ.can ~ Normal (0, 0.001) and τβ.can, that is the inverse of variance (τβ.can = sdβ.can-2), where sdβ.can ~ Uniform (0, 10), and these hyper-parameters are shared by all species in this stratum (Yamaura et al., 2016). Similarly, we determined the mean and standard deviation for understory parameters (β.und) and the slope (β1) of biological process, as well for parameters of observational process (α1 and α2). We define that α.cank and α.undk ~ Normal (µα.can, τ α.can), but to avoid the yielding of informative priors we set the µα.can  = logit(µα.can.pre), when µα.can.pre ~ Uniform (0, 1). The model was run using the package *jagsUI* (v. 1.4.9, Kellner, 2017) with three Markov Chains Monte Carlo (MCMC), 230,000 iterations with the first 30,000 iterations discarded and a thinning rate of 200. These settings of MCMC results in a posterior sampling with 3,000 iterations. We also defined initial values for parameter N and monitored the community mean and species-level parameters. We checked the convergence of MCMC graphical visualization (Appendix 1) and in addition we simulate communities with differ initial parameters of interest, aiming to validate the Bayesian model. The scripts of the Bayesian model and for simulations are available on Github (xxxx) and as supplementary information (Appendix 2).

*Phylogenetic and functional data*

We collected at least one specimen of each butterfly species captured in bait traps for subsequent measurement of functional traits. We selected 13 functional traits to characterize functional diversity in each community, including traits related to flight performance, habitat use and ecological behavior (Table 1) (Chai & Srygley, 1990; Dudley, 2002; Spaniol, Duarte, Mendonça, & Iserhard, 2019). Using the recently proposed phylogeny of Chazot et al. (2019) for Nymphalidae, we obtained the phylogenetic relationships among the 35 species of fruit-feeding butterflies recorded in this study. The pruned tree was employed to calculate the subsequent analysis of phylogenetic diversity and structure of communities. We used the packages *ape* (v. 5.3, Paradis, 2018), and *phytools* (v. 0.6-44, Revell, 2012) to prune the tree.

We tested the relationship between detection probability (p) for each stratum and the mean traits of species, aiming to evaluate if the detection can be predicted by traits. If p is predicted by any traits, we tested for phylogenetic signal for this trait using K statistics. High phylogenetic signal (K > 1) means that species detection probability, moderated by the functional trait, is more phylogenetically constrained than expected by random sampling of the species pool (Blomberg, Garland, & Ives, 2003). To evaluate which traits were most related to the detection probability in either the canopy or the understory we employed phylogenetic independent contrasts (PIC, Felsenstein, 1985). This model allows including phylogenetic covariance among species, and thus controls for phylogenetic non-independence (Blomberg et al. 2003), assuming Brownian model of trait evolution. We performed a simple linear model (OLS) between the PICs of the detection probabilities and PICs of traits for each stratum. Traits showing variance inflation factors (VIF) greater than three were removed from models; thus, eight traits were kept to perform the OLS. The Brownian correlation structure and PIC models were calculated using the package *ape* (v. 5.3, Paradis, 2018).

*Incorporating imperfect detection in diversity measures*

To evaluate the magnitude of the effects of imperfect detection on diversity measures we developed a R function called *hidden.diversity* (Supplementary information, Appendix 3). This function returns, for each site *i*, the ratio between the deviation of observed diversity from the estimated diversity, given imperfect detection, and the standard deviation of the estimated diversity:

Where *div.obsi* is the taxonomic, functional or phylogenetic diversity value obtained with raw count data for each site, is the mean diversity value obtained from *Nik* posterior sampling in each site and *sd.div.esti* is the standard deviation of *div.esti*. Negative values indicate an underestimation of observed diversity values in relation to estimated diversity values, indicating that there is more diversity than we observed. When hidden diversity assumes positive values, it indicates that observed diversity values are overestimated in relation to estimated values. This last situation can only occur for phylogenetic/functional measures, and indicates that undetected species are redundant, i.e. they are already covered by sampling. Values near zero indicate small differences between raw and estimated diversities values.

The input of the *hidden.diversity* function is the observed community data, a phylogenetic tree, a matrix containing the mean traits for each species and the matrix *Nik* informing the posterior samples of the Bayesian model. The function internally calculates taxonomic diversity (TD), the standardized effect size for phylogenetic diversity (SES.PD) and for functional diversity (SES.FD), as well as the SES for phylogenetic and functional structure (SES.MPD and SES.MFD respectively). Also, the function allows indicating if there are binary data in the trait matrix, if the diversity measures should be weighted by abundance, the type of null model and the number of permutations used to calculate the null models. The null models are randomized communities simulated based on models implemented in the package *picante*, that aim to remove the effect of richness in the diversity measures. The function output is an SES value for each site, controlling for both imperfect detection and richness effects.

**Results**

Our database contained 35 species and 914 individuals of fruit-feeding butterflies, which had higher community-level mean abundance in the understory than in the canopy (µβ.can = 5.608, CRI95% = 1.865 to 6.778, µβ.und = 5.783, CRI95% = 1.919 to 6.981). Moreover, understory assemblages also had a higher mean detection probability, without considering the effects of sampling months (µα.can = 0.028, CRI95% = 0.009 to 0.034, µα.und = 0.635, CRI95% = 0.561 to 0.717) (Supplementary information, Fig. A1). This result implies that detection probability was not constant between canopy and understory (Fig 1c, d).

The species-specific prediction demonstrates that the most species in the canopy tended to increase their expected abundance as temperature increased (Fig. 2a), except for one species that decreased abundance with higher temperature. The detection probability in this stratum showed two peaks, with two species being more detectable between November and December, while all others tended to increase detection probability during summer months (January to March in the south hemisphere) (Fig. 2c). On the other hand, species in the understory exhibited greater variation in their abundance responses to temperature, with the majority having an expressive increase at higher temperatures, while two species had lower than expected abundances under higher temperatures (Fig. 2b). All but one species in this stratum had a peak of detection in January, while the exception experienced a decrease in detection in this month (Fig. 2d). We did not find a strong correlation between detection probability and raw counts for canopy (rho = 0.488, p = 0.002) or understory (rho = 0.489, p = 0.003) assemblages.

We did not find phylogenetic signal for mean detection probability for the canopy (K= 0.302) or understory (K= 0.276), indicating that species detection is not an artefact of the phylogenetic relationships among species (Supplementary information Fig. A2). We observed a positive effect for aspect ratio on detection probability in the canopy (Fig. 3a, Table 2), and for abdomen mass in the understory (Fig. 3b, Table 2).

Hidden diversity demonstrated that all diversity measures had similar behavior among strata when incidence data were used, with most cases being underestimated (negative values of hidden diversity) or overlapping zero (Fig. 4). When we did not consider imperfect detection, the phylogenetic and functional measures had lower losses of information than did taxonomic diversity (both richness and abundance). However, abundance-weighted phylogenetic and functional diversity exhibited greater variation in the values for canopy than in the understory, and some sites had slight overestimations for both metrics (positive values of hidden diversity). This overestimation indicates that the undetected individuals were phylogenetically closer and shared similar phenotypic features with individuals sampled in the canopy, leading to a bias in diversity values for one level of the vertical gradient.

**Discussion**

Our results demonstrate a loss in information for all the diversity measures analyzed, but individual detection probability was asymmetric for canopy and understory, which was highly relevant when we used count data to estimate functional or phylogenetic measures. Under this scenario, and even when an association between detection probability and phylogenetic/trait-based relatedness among species is lacking, the inclusion of individuals could cause large variation in hidden diversity since uncertainty is high. We also observed that diversity patterns associated with part of the environmental gradient, canopy in this case, might be biased by imperfect detection, which warns us of the relevance of considering uncertainty in the sampling process of analyses aiming to evaluate diversity-environment relationships. Despite this, when incidence-base data were employed to calculate diversity measures the values were underestimated for both strata, but the pattern remained the same. Since accounting for imperfect detection improves the accuracy of estimates of diversity patterns, in some circumstances it is strongly recommended (Fig 1c, d), because it may lower the risk of erroneously inferring biological processes that are implied by sampling uncertainty (Joseph et al., 2009). If detection probability is constant, then the raw data is likely to detect the true diversity pattern in assemblages, even if the information is incomplete.

As expected, canopy assemblages had lower detection probabilities than understory assemblages, and detection was associated with traits related to dispersal. Canopy-dwelling fruit-feeding butterflies generally show higher energy allocation to flight traits (Chai & Srygley, 1990, Schulze et al., 2001, Berwaerts et al., 2002) and are also more vagile than understory species (Hill et al., 2001; Pedrotti et al., 2019). Such high mobility was associated with individual detection in canopy sites because the individuals are more dispersive, while less mobile individuals were undetected. However, the canopy tended to have higher sample coverage of butterfly fauna with regard to species richness, and species accumulation occurred faster than in the understory (DeVries et al., 2012, Santos et al., 2017). This faster species accumulation in the canopy could cause less bias when only occurrence data is employed to evaluate diversity measures between strata, because species diversity was considered. On the other hand, butterflies that inhabit the understory have higher energy allocation to abdominal mass, which is an improvement in reproductive investment (Schulze et al., 2001, Pedrotti et al., 2019). We observed that the detection probability increased considerably in the understory in warmer months (December to February in the Southern Hemisphere), which is the optimal climatic window for fruit-feeding butterflies in the subtropical region (Iserhard et al., 2017). Individual recruitment is high during this period due to increased food availability for immatures and adults (Ribeiro & Freitas, 2011), promoting resource allocation to reproductive tissues. Thus, the understory is expected to exhibit more consistent abundance-weighted diversity patterns than the canopy when imperfect detection is accounted for in the computation of phylogenetic and functional measures, at least in short-term studies, like the present, that include the optimal climatic window.

In contrast to previous studies, we did not find strong variation in phylogenetic and functional diversity patterns when imperfect detection was considered, at least for incidence-based measures (SES.PD/FD and SES.MPD/MFD). For incidence data of bird assemblages, taxonomic (alpha and beta, Tingley and Beissinger 2013), functional and phylogenetic measures (Si et al., 2018) were underestimated when imperfect detection was not taken into account. If undetected species have unique evolutionary histories and/or functional traits, we would expect to observe assemblages that are more clustered than they really are (Jarzyna & Jetz, 2016, Si et al., 2018), and therefore the mechanisms that structure such assemblages could be erroneously interpreted (Frishkoff et al., 2017). Additionally, Frishkoff et al. (2017) suggested that parameters estimated considering imperfect detection increase the phylogenetic signal among species and environmental gradients. In the present study, we observed that detection probability was not related to phylogenetic relationships among species in either of the strata. Thus, it is not surprising that we did not find drastic changes in phylogenetic measures, nor in the inference of assembly mechanisms, at least for incidence data. On the other hand, functional measures were slightly distinct among strata, which could be an artifact of variation in detection probability of species that have specific traits (Roth et al., 2017). Furthermore, the above-mentioned studies considered larger spatial scales than used in the present study. Thus, we suggest that the effect of imperfect detection on abundance-based, and not on incidence-based, measures could be an outcome of spatial scale, and that this association among imperfect detection, richness and abundance and spatial scale is an interesting subject for future studies.

Biodiversity measures are important tools to guide species conservation decisions, as well as to infer about ecological and evolutionary process that structure assemblages. Several models have been proposed in recent years to incorporate imperfect detection in order to improve the efficiency of estimating parameters in community studies (Zipkin et al., 2010, Banks-Leite et al., 2014, Frishkoff et al., 2014, Jarzyna & Jetz, 2016). However, as suggested by Banks-Leite et al. (2014), despite the large power of hierarchical occupancy or abundance models, *a posteriori* adjustments of imperfect detection cannot amend uncertainties related to poor sampling design. Thus, standardized and robust sampling designs should be prioritized to ensure that diversity patterns can be appropriately captured in the field (Freitas et al., 2020). In this context, employing hierarchical model of occupancy/abundance to evaluate the consistency of species/individual detection along environmental gradients is complementary to well conducted field sampling, rather than a solution to fix poor field sampling.

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